Field Crops Research, 17 (1987) 273-288
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

Physiological Basis for Yield Advantage in a Sorghum/Groundnut Intercrop Exposed to Drought.*
2. Plant Temperature, Water Status, and Components of Yield

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(Accepted 5 August 1987)

ABSTRACT

Harris, D. and Natarajan, M., 1987. Physiological basis for yield advantage in a sorghum/groundnut intercrop exposed to drought. 2. Plant temperature, water status, and components of yield. *Field Crops Res.*, 17: 273-288.

In a replacement series intercrop of two rows of groundnut (cv. Kadiri 3) alternating with one row of sorghum (hybrid CSH-8), increases in grain and filled-pod weight per plant due to intercropping were large, especially in droughted stands. For sorghum, grain yields were 38% and 93% higher per unit row in the well-watered and droughted treatments respectively, while intercropped groundnut produced 81% more filled-pod weight per unit row than did sole stands during drought. Harvest index was larger for both species in the intercrops, by 8% and 33% in 'wet' and 'dry' sorghum, and by 12% and 68% in 'wet' and 'dry' groundnut. In groundnut, harvest index was increased in the 'wet' intercrop because individuals pods were heavier, whereas the 'dry' intercrop produced twice as many pods per plant in comparison with the sole crop.

There were large differences in plant temperature and water status between 'wet' and 'dry' stands throughout the post-rainy season, but mean differences between sole crops and intercrops within each water regime were small. However, shading of groundnut by sorghum in the intercrop ameliorated to some extent the effects of high temperature and water stress, especially in the droughted stands. This was particularly important during peg production. It is suggested that less damage to flowers in the 'dry' intercrop resulted in more pegs forming pods than in the 'dry' sole crop, leading to the observed advantage in harvest index in groundnut.

Submitted as Journal Article No 652 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).
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0378-4290/87/$03.50

INTRODUCTION

Some workers have shown that relative yield advantages from intercrops are larger when resources such as water or nutrients are scarce (Chang and Shibles, 1985a,b; Natarajan and Willey, 1986). Recent work on intercrops of cereals and legumes suggests that, although total dry matter is often increased by intercropping, increases of economic yield, when they occur, are a consequence of more favourable allocation of dry matter to reproductive structures. This effect increases with drought (Natarajan and Willey, 1986; Harris et al., 1987b, this volume).

Increases in total dry matter are associated with the interception of more light and more efficient use of light in a number of intercrops (Marshall and Willey, 1983 for millet (*Pennisetum typhoides* S. & H.) and groundnut (*Arachis hypogaea* L.); Willey and Natarajan, 1980 for sorghum (*Sorghum bicolor* L.) and pigeonpea (*Cajanus cajan* L.); Harris et al., 1987b for sorghum and groundnut). However, far less attention has been paid to the importance of radiation in determining canopy temperature and water status, despite several theoretical reviews (Allen et al., 1976; Trenbath, 1976). Since rates of plant development are governed by temperature and water status (Ong., 1984; Harris et al., 1987a), changes in these variable as a result of intercropping could account for the differences in allocation of dry matter. In this paper, we investigate this possibility in an intercrop of sorghum and groundnut and sole-crop stands of both species.

MATERIALS AND METHODS

Experimental design

Sole crops and an intercrop of sorghum and groundnut were grown at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Center, Patancheru, India (17°38′N, 78°21′E). Sorghum (hybrid CSH-8) and groundnut (cv. Kadiri 3, formerly known as Robut 33-1) were sown on 23 December, 1983, in rows 30 cm apart and thinned 3 weeks later to 20 cm within rows for sorghum (16.6 plants m^{-2}) and 10 cm within rows for groundnut (33.3 plants m^{-2}). All rows were orientated NW–SE. The intercrop consisted of one row of sorghum alternating with two rows of groundnut, with each component at the same within-row spacing as in the sole crop. Irrigation was by line-source sprinkler (Hanks et al., 1976). Within the gradient of water supplied, two regimes, 'wet' and 'dry', received totals of 460 mm and 263 mm of water, respectively. To achieve this, 120 mm water was applied to all crops between sowing and 35 days after sowing (DAS), and line-source irrigations were applied at 48, 60, 71, 90, 98 and 111 DAS. A further uniform irrigation was applied at 78 DAS when 26 mm rain also fell. Each cropping system/water application combination was replicated four times within a randomised block design. Further details of crop management and experimental design are given by Harris et al. (1987b).

Groundnut temperature measurements

Eight groundnut plants per water regime (two per replicate) were chosen at random from both sole and intercrop. Two fine (38 swg) copper-constantan wire thermocouples were inserted into the main stem of each plant, one directly below the apical meristem, the other at the base of the main stem adjacent to the cotyledonary branches. This latter position was chosen to represent tissue temperature close to where pegs were developing, the 'peg zone'. A third thermocouple was buried 3 cm below the soil surface underneath each plant to measure the pod-zone temperature. The thermocouples were connected to an electronic thermometer (Model 1625, Comark Electronics Ltd*). Measurements were made every hour from 0800–1800 Indian Standard Time (IST) on twelve dates between 41 and 89 DAS.

Leaf water potential

Leaf water potential (Ψ_l) was measured in sorghum on 8 days from 67 to 96 DAS, and in groundnut on 8 days from 44 to 91 DAS. Every 2 h between 0700 and 1700 IST, Ψ_l of two leaves from the top, middle and bottom of each canopy were measured in each treatment using a pressure chamber (PMS Instrument Company, Corvallis, Oregon*).

Growth analysis

Plants were harvested for growth analysis at 25, 48, 73, 81, 90 and 126 DAS (groundnut) and 31, 48, 60, 73, 81, 90 and 108 DAS (sorghum). Data from one of the 4 replicates were discarded because of unrepresentative growth in a plot with non-uniform soil and heavy infestation with *Striga* on sorghum. Weights and numbers of plant components are expressed both on a per-unit field-area basis and as crop performance ratios (CPR), defined as $I/(S \cdot p)$ where I and S are weights or numbers of plant elements per unit area sown with that component in the intercrop and sole crop, respectively, and p is the corresponding proportion sown in the intercrop.

The total crop performance ratio (TCPR) is the sum of the weights or numbers of that element in the intercrop ($I_s + I_g$) expressed as a fraction of the

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*Mention of commercial products or companies does not imply endorsement or recommendation by ICRISAT of these over others of a similar nature.

same quantity in the two sole crops, i.e. $(S_s \cdot p_s) + (S_g \cdot p_g)$ where the subscripts s and g refer to sorghum and groundnut, respectively (Harris et al., 1987b).

The performance of intercrop components is often discussed in this paper relative to an 'expected' performance based on results from the appropriate sole stand. Expected results are calculated as the value per unit area obtained in the sole stand, multiplied by the sown proportion of that component in the intercrop.

RESULTS

Botanical measurements

Tables 1 and 2 show final harvest data for all reproductive elements of sole and intercropped groundnut and sorghum. For groundnut (Table 1), intercropping was associated with differences in both vegetative and reproductive production (economic yield) relative to the sole crop. In terms of CPR, Table 1 shows a 3% decrease for filled pod weight in the wet treatment but an 81% increase in the dry treatment. Similarly, large CPR values were obtained in the dry treatment for all components of yield except vegetative dry weight and individual filled-pod weight.

Because filled-pod weight is the product of the filled-pod number and the mean weight of individual pods, the following equation can be used to identify the relative contribution of each yield component to yield advantage:

harvest index = (pod number × weight per pod)/total dry matter

Using the CPR values from Table 1, the relative effects of intercropping on development (pod number) and growth (weight per pod and total dry matter) could be estimated for both wet and dry regimes as follows:

Wet $(0.88 \times 1.11)/0.88 = 1.11$
Dry $(2.01 \times 0.91)/1.08 = 1.69$

These are consistent with values for harvest indices in Table 1.

In the wet treatment, the harvest index CPR of 1.12 was entirely due to increased weight per pod, since the reductions in pod numbers and total dry matter were the same. Conversely, the large CPR for harvest index in the dry treatment was mainly a consequence of the large CPR for filled-pod number. It was not recorded whether or not this was due to differences in the numbers of seeds per pod.

In sorghum (Table 2), intercropping increased allocation to reproductive structures in both wet and dry treatments, and only vegetative dry weight in the dry treatment had a CPR less than 1.0. Again, the harvest index advantage

TABLE 1

Components of groundnut yield (g m^{-2} unless indicated otherwise) and crop performance ratios for sole crops and intercrops - see text for explanation

	Wet			Dry			CV (%)
	Sole	Inter	CPR	Sole	Inter	CPR	
Total pod no.	410	235	0.87	187	178	1.44	10.7
Filled pod no.	350	203	0.88	72	95	2.01	13.1
Filled pod wt.	317	205	0.97	56	67	1.81	9.9
Indiv. filled pod wt. (g pod^{-1})	0.91	1.01	1.11	0.78	0.70	0.91	4.7
Total pod wt.	334	213	0.96	77	85	1.67	14.0
Indiv. pod wt. (g pod^{-1})	0.82	0.91	1.10	0.41	0.48	1.16	7.0
Kernel wt.	239	159	1.01	42	45	1.61	16.9
Veget. dry wt.	404	218	0.82	322	198	0.93	8.9
Total dry matter	739	431	0.88	399	283	1.08	7.4
Kernel HI	0.32	0.37	1.16	0.10	0.16	1.60	8.4
Filled-pod HI	0.43	0.47	1.12	0.14	0.24	1.68	9.6

Coefficients of variation (CV) are based on analysis of variance of intercrop data and expected values in the sole crops if CPR = 1.

in the dry treatment was greater than that in the wet, but a more detailed analysis of yield components was not possible for logistical reasons.

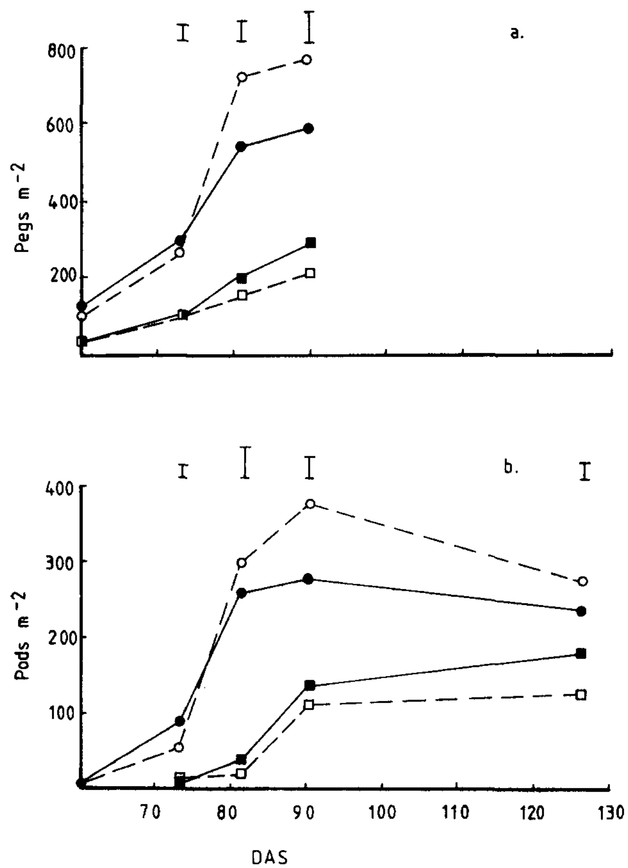
Allocation of dry matter in groundnut was examined further. Figure 1 shows the time course of expected and actual numbers of pegs and pods in the intercrops. Pegs were more numerous than expected in the dry intercrop after 73 DAS, but were fewer than expected in the wet intercrop. The same trend was apparent for pod number after 81 DAS. (Note that total pod number is plotted, whereas filled-pod number, a category recognised only in the later harvests, is

TABLE 2

Components of sorghum yield (g m^{-2}) and crop performance ratios for sole crops and intercrops - see text for details

	Wet			Dry			CV (%)
	Sole	Inter	CPR	Sole	Inter	CPR	
Panicle weight	609	276	1.37	253	164	1.97	7.9
Grain weight	502	228	1.38	206	131	1.93	8.8
Veget. dry weight	369	139	1.14	279	87	0.95	8.8
Total dry matter	978	415	1.29	532	252	1.43	6.8
Harvest index	0.52	0.55	1.08	0.39	0.52	1.33	8.1

Coefficients of variation (CV) are based on analysis of variance of intercrop data and expected values in the sole crops if CPR = 1.



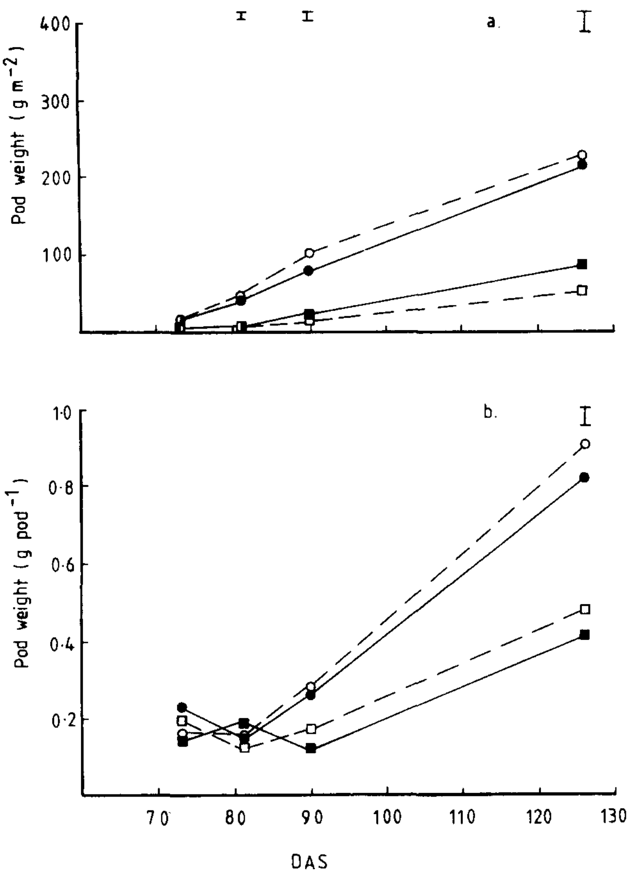


Fig. 2. Expected and actual pod dry weight (a) per m^2 and (b) per pod in the wet and dry intercrops. Symbols as in Fig. 1. Standard errors are included only where there were significant differences between treatments.

given in Table 1). The reason for decreases in numbers in the wet treatments between 90 and 126 DAS is unknown.

Expected and actual total pod weight per unit area in the intercropped groundnut is shown in Fig. 2a. The intercropped groundnut consistently produced less total pod weight than expected in the wet treatment but more in the dry. Mean individual pod weights plotted in Fig. 2b show that pods were smaller in the intercrops under both water regimes from 90 DAS onwards, and the CPR for mean filled-pod weight was only 0.97 in the wet treatment (Table 1).

The relation between the number of pegs and the number of pods per unit

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Fig. 1. (a) Peg numbers m^{-2} and (b) pod numbers m^{-2} for groundnut in the dry and wet intercrop treatments: dry: expected □, actual ■; wet: expected ○, actual ●. Vertical bars are standard errors of observed values.

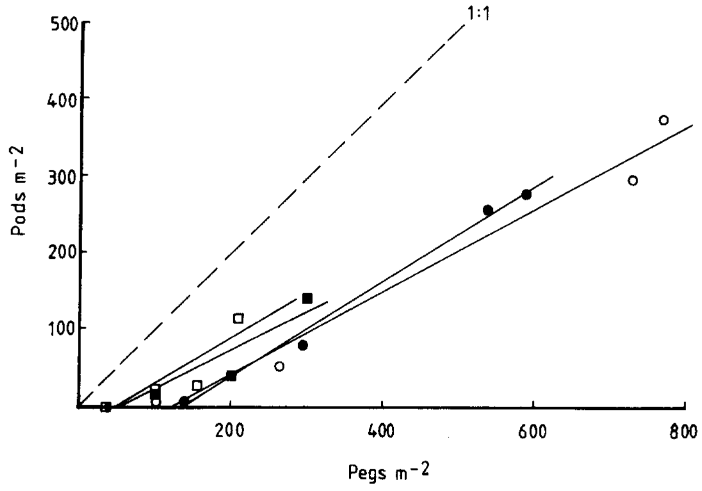

Fig. 3. The relation between groundnut pod number (y) and peg number (x) for all treatments. The dashed line represents a 1:1 ratio. Linear regressions fitted to the data are as follows:

Dry sole crop (■)	$y=0.60x-34$;	$r^2=0.76$;	($n=4$)
Dry intercrop (□)	$y=0.51x-32$;	$r^2=0.876$;	($n=4$)
Wet sole crop (●)	$y=0.53x-68$;	$r^2=0.97$;	($n=4$)
Wet intercrop (○)	$y=0.62x-90$;	$r^2=0.99$;	($n=4$)
Overall	$y=0.51x-38$;	$r^2=0.95$;	($n=16$)

There was no significant effect of treatments on the slope or intercept.

area is shown in Fig. 3. Analysis of variance of linear regressions fitted to the data showed no significant differences among the treatment/crop combinations in either the rate (slope) or the threshold peg number for conversion of pegs to pods. Thus, differences in pod number between sole and intercrops are a direct consequence of differences in peg number illustrated in Fig. 1.

Physical measurements

Mean leaf water potentials (Ψ_l) of sorghum and groundnut during daylight hours are shown in Fig. 4. All groundnut stands in the wet treatment maintained higher values (closer to zero) of Ψ_l than dry stands thoughout the period 44–91 DAS except on 88 DAS. Although Ψ_l in the wet intercrop did not differ from that in the wet sole crop, in the dry intercrop it was always higher than in the dry sole crop (except on 80 DAS following a uniform irrigation), even after the rain and irrigation at 78 DAS. Patterns of Ψ_l in time for sorghum were similar to those for groundnut, although the difference between wet and dry stands was far less marked. In general, water potentials were somewhat higher in intercropped sorghum under both irrigation regimes. Mean values of Ψ_l for the whole of the period are shown in Table 3. Although intercrops were

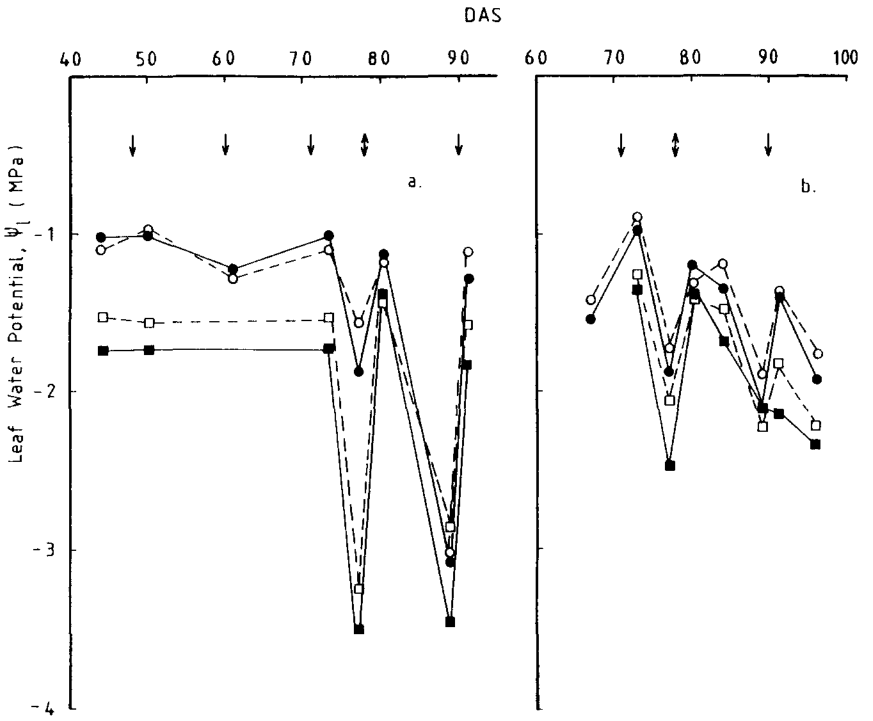

Fig. 4. Mean leaf water potentials during daylight hours of groundnut (a) and sorghum (b). Sole crop wet, ●; intercrop wet, ○; sole crop dry, ■; intercrop dry, □; line-source irrigation, ↓; uniform irrigation, ↕.

less stressed than sole crops in all cases, the differences were small compared to those between wet and dry crops.

Figure 5 shows the mean daily difference between plant and air temperature for the apical meristem and peg zone, and between air and soil temperature in

TABLE 3

Mean leaf water potentials (MPa) during daylight hours

	Sorghum		Groundnut	
	Wet	Dry	Wet	Dry
Sole crop	−1.56 (0.36, 8)	−1.94 (0.41, 7)	−1.48 (0.67, 8)	−2.21 (0.83, 7)
Intercrop	−1.46 (0.31, 8)	−1.80 (0.37, 7)	−1.44 (0.63, 8)	−1.97 (0.71, 7)

Figures in brackets are standard errors of each mean, followed by the number of days comprising the mean.

the pod zone of groundnut for the period 41–98 DAS. The difference between plant and air temperature (Fig. 5) is a good indicator of stress because it reflects the degree to which plants are able to dissipate energy by evaporation. Using the temperature difference also allows comparison between treatments throughout the season, relatively independent of variation in irradiance and air temperature. Differences in temperature differential between sole and intercrops were small and inconsistent within water regimes, but wet stands were always cooler than dry stands (except in two cases on 41 DAS and in one on 89 DAS). Temperature always fell following an irrigation. At any sampling date the temperature differential tended to be largest for the meristem, intermedi-

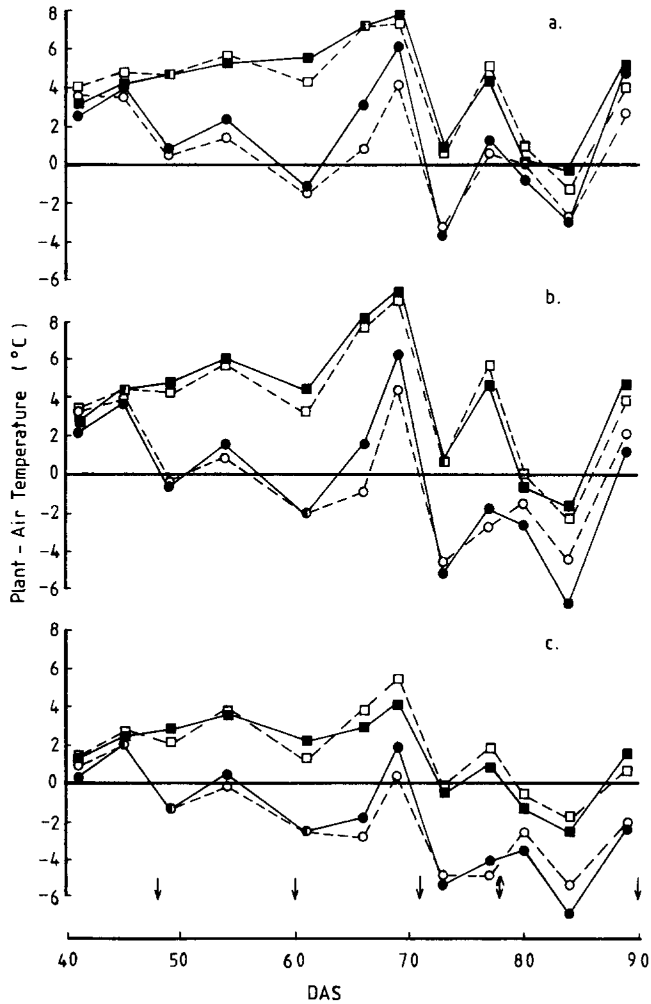

Fig. 5. Mean daily plant-air temperature difference for groundnut (daylight hours only). a, meristem; b, peg zone; c, pod zone. Symbols as in Fig. 4.

ate for the peg zone and lowest for the pod zone. This may be the result of shading both by sorghum in the intercropped groundnut and by the groundnut canopy itself in both cropping systems. The exceptions on 54 and 69 DAS occurred towards the end of an irrigation interval when the upper leaflets of groundnut were folding in response to stress, resulting in penetration of radiation deeper into the crop. The actual daily mean air temperatures experienced by the stands ranged from around 25–26 °C on 45 and 54 DAS to around 32 °C on 89 DAS, although diurnal variation about these means was large (Fig. 6). Overall mean differences of temperature between cropping systems were small and not significant compared to those between irrigation regimes (Table 4).

Figure 6 shows the diurnal course of meristem temperature in dry sole-crop and intercropped groundnut on two days. On the first date (41 DAS) when shading from the young sorghum was still negligible, intercrop meristem temperatures were higher than those of the sole crop, possibly because sorghum sheltered the groundnut from the wind, reducing turbulent mixing. Visual observations of leaf movement in both crops tended to support this speculation, and further work is in progress to test it. Once significant shading began (61 DAS, Harris et al., 1987b) intercrop temperatures were consistently lower than those of the sole crop.

Figures 7a and b show the diurnal course of Ψ_l of the last fully expanded leaf on 77 DAS in groundnut and sorghum, respectively. This was the day before the irrigation on 78 DAS and stress was severe, especially in the dry treatments.

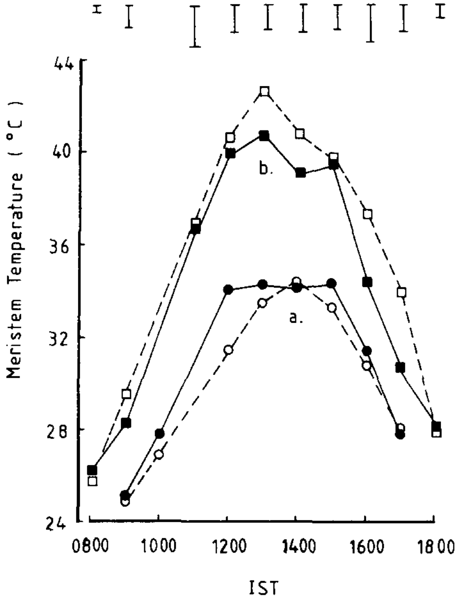

Fig. 6. Diurnal course of groundnut mersitem temperatures in the dry sole crop and intercrop on 41 DAS (●,○) and 61 DAS (■,□). Filled symbols, intercrop; open symbols, sole crop.

TABLE 4

Mean groundnut temperatures (°C) during daylight hours over the experiment between 41 and 89 DAS

	Wet			Dry		
	Meristem	Peg	Pod	Meristem	Peg	Pod
Sole crop	29.9 (3.1)	28.3 (2.8)	26.6 (1.8)	32.6 (2.8)	32.4 (3.0)	30.0 (1.9)
Inter-crop	29.2 (2.4)	28.3 (2.7)	26.6 (1.7)	32.5 (2.5)	32.4 (2.9)	30.2 (1.9)

Figures in brackets are standard errors of each mean ($n = 12$).

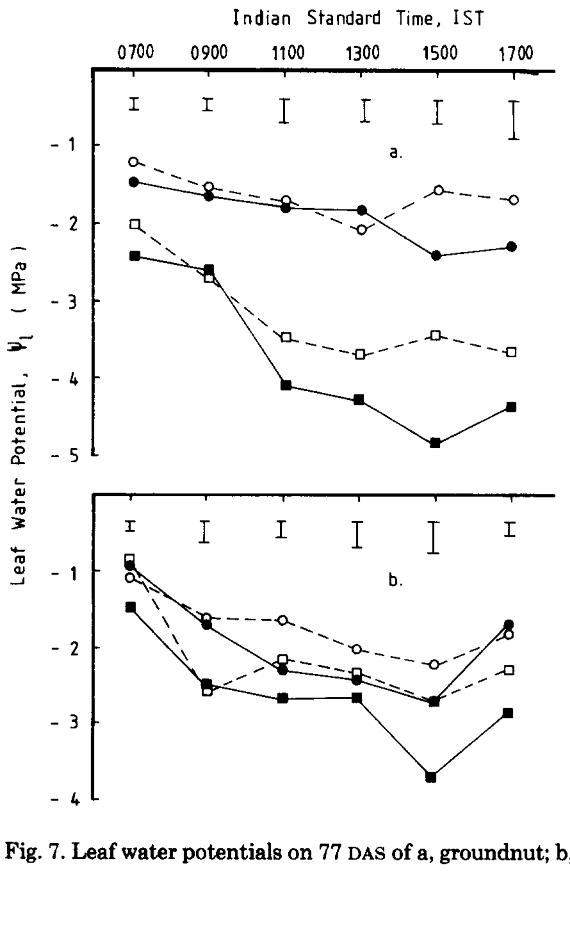

Fig. 7. Leaf water potentials on 77 DAS of a, groundnut; b, sorghum. Symbols as in Fig. 4.

Values of Ψ_l decreased in all treatments in the course of the day, and leaves of both intercrops maintained higher values of Ψ_l than the sole crops. This pattern emerged to a greater or lesser extent on all sampling dates. Conditions on 76 DAS were very similar and the data for 0700 in Fig. 7 can be treated as an estimate of the extent of recovery after a stressful day. This suggests that recovery was more complete in sorghum than in groundnut, although the degree of stress suffered by sorghum was less to begin with.

DISCUSSION

Numbers of reproductive structures per plant are important in producing yield advantages from intercropping because they determine the size of the sink for assimilate allocated to reproductive structures (Osiru and Willey, 1972; Faris et al., 1983). For a given sink size, actual yield then depends upon the supply of assimilate or source size. Analysis of yield components in this experiment shows that the 12% advantage for filled-pod harvest index in the wet intercropped groundnut was due to increased weight per pod, representing an increased source size which was offset, however, by a decrease in sink size. In contrast, most of the 68% advantage in the dry intercropped groundnut could be attributed to a doubling in the number of pods per plant (increased sink size) while weight per pod (source size) was reduced only slightly. Thus, patterns of resource allocation in groundnut were different in the wet and dry intercrops. Since these differences became apparent before the harvest of the sorghum at 108 DAS, they may be ascribed to some form of 'spatial complementarity' between the two components of the intercrop (Willey, 1979). However, an unknown proportion of yield advantage in groundnut may have been a consequence of growth after DAS at a reduced population density and would represent 'temporal complementarity'.

Rates of phenological development in groundnut are primarily governed by temperature (Leong and Ong, 1984) and to a lesser extent by water status (Harris et al., 1987a). Ong (1984) showed that for groundnut growing in controlled environments the ratio of pod to shoot weight (PWR) was highest at 22 °C and decreased as temperature increased to 31 °C. Pod: shoot weight ratio was also negatively correlated with the ratio of stem dry weight to total dry weight, suggesting that the balance of competition between alternative sinks was altered by temperature: lower temperature favoured production of pegs and pods at the expense of leaves and stems. Unfortunately, no observations were made above a mean temperature of 31 °C. Temperature gradients can develop from top to bottom of groundnut plants in the field (Fig. 5), and it is likely that the lower temperatures in the wet treatment favoured peg and pod production and led to the large harvest indices relative to the dry treatment (Table 1).

Pod:peg ratios were not significantly different in the sole and intercrops. Peg number in groundnut is a function of the number of flowers produced and its proportion producing pegs. Successful fertilization of flowers in legumes may be inhibited by high temperatures and water deficits (Lee et al., 1972; Bhatia et al., 1984) and, in this experiment, most peg development took place between 50 and 90 DAS when plant temperature was increasing and water status was decreasing to daily mean values below −3.0 MPa (Fig. 4). Since flower production and fertilization in groundnut occurs in the early morning (Nigam et al., 1980), then the increased peg production by the dry intercrop may well have been due to shading by sorghum during this part of the day and, consequently, to the lower temperatures and higher water potentials relative to the dry sole-crop groundnut. Observations of leaf-wilting in the dry treatment indicated that intercropped groundnut did benefit from a period of reduced stress (relative to the sole crop) early in the morning when the sun was low and shading by sorghum was most pronounced. Later in the day Ψ_l declined, and plant temperatures increased to supra-optimal levels (i.e. above about 30°C: see Leong and Ong, 1983) at which rates of developmental processes in groundnut are slowed.

Natarajan and Willey (1986) suggested that the better performance of sorghum in the intercrops was due to a reduction in the level of competition between sorghum plants at the lower population density. Figs. 4b and 7b suggest that the level of water stress was lower in the intercropped sorghum. It cannot be concluded, however, whether sorghum could either extract more water when in competition with the groundnut, or extract the same amount but maintain higher Ψ_l, thus minimising possible effects on rates of growth and development. Both total dry-matter production and partitioning to reproductive structures were increased in intercropped sorghum, but it was not possible to analyse the yield components as we did for groundnut.

Research on intercropping has increased in recent years (Willey, 1979), although little information is available on the effects on microclimate. The measurements described here and by Harris et al. (1987b) suggest that intercropping sorghum with groundnut altered the microclimate, resulting in some subtle physiological responses. Radiation interception and use, plant temperature, Ψ_l, and possibly the balance of water extraction between the component crops, were all affected. Economic yields were increased by using this intercrop system, especially in the dry treatment, and we feel that further investigation of these effects is required to identify specific traits which could be used to design successful intercropping systems matched to a range of environments. To this end, systematic examination of intercropping systems should include measurements of plant microclimate wherever possible.

ACKNOWLEDGEMENT

The authors thank Prof. J.L. Monteith, Prof. R.W. Willey and P.F. Harris for their help and encouragement, and an anonymous referee for his tolerance. The support of ICRISAT and the Overseas Development Administration is gratefully acknowledged.

REFERENCES

Allen, L.H., Sinclair, T.R. and Lemon, E.R., 1976. Radiation and microclimate relationships in multiple cropping systems. In: R.I. Papendick, P.A. Sanchez and G.B. Triplett (Editors), Multiple Cropping. Am. Soc. Agron. Spec. publ. 27, Madison Wis., pp. 171-200.

Bhatia, V.S., Bhargava, S.C. and Sinha, S.K., 1984. Effect of irrigation on reproductive efficiency of bunch and spreading types of groundnut (*Arachis hypogaea* L.) J. Agric. Sci., Camb., 102: 505-508.

Chang, J.F. and Shibles, R.M., 1985a. An analysis of competition between intercropped cowpea and maize. 1. Soil N and P levels and their relationship with dry matter and seed productivity. Field Crops Res., 12: 133-144.

Chang, J.F. and Shibles, R.M., 1985b. An analysis of competition between intercropped cowpea and maize. 2. The effect of fertilization and population density. Field Crops Res., 12: 145-152.

Faris, M.A., Burity, H.A., Dos Rios, O.V. and Mafra, R.C., 1983. Intercropping of sorghum or maize with cowpea or common beans under two fertility regimes in northeastern Brazil. Exp. Agric., 19: 251-261.

Hanks, R.J., Keller, J., Rasmussen, V.P. and Wilson, D.G., 1976. Line source sprinkler for continuous variable irrigation-crop production studies. Soil Sci. Soc. Am. J., 40: 426-429.

Harris, D., Matthews, R.B., Nageswara Rao, R.C. and Williams, J.H., 1987a. The physiological basis for yield differences between four genotypes of groundnut (*Arachis hypogaea* L.) in response to drought. 3. Developmental processes and yield. Exp. Agric. (in press).

Harris, D., Natarajan, M. and Willey, R.W., 1987b. Physiological basis for yield advantage in a sorghum/groundnut intercrop exposed to drought. 1. Dry matter production, yield, and light interception. Field Crops Res., 17: 259-272.

Lee, T.A., Jr., Ketring, D.L. and Powell, R.D., 1972. Flowering and growth response of peanut plants (*Arachis hypogaea* L. cv. Starr) at two levels of relative humidity. Plant Physiol., 49: 190-193.

Leong, S.K. and Ong, C.K., 1983. The influence of temperature and soil water deficit on the development and morphology of groundnut (*Arachis hypogaea* L.). J. Exp. Bot., 34: 1551-1561.

Marshall, B. and Willey, R.W., 1983. Radiation interception and growth in an intercrop of pearl millet/groundnut. Field Crops Res., 7: 141-160.

Natarajan, M. and Willey, R.W., 1986. The effects of water stress on yield advantages of intercropping systems. Field Crops Res., 13: 117-131.

Nigam, S.N., Dwivedi, S.L. and Gibbons, R.W., 1980. Groundnut breeding at ICRISAT. In: Proc. International Workshop on Groundnuts, 13-17 October, 1980, Patancheru, A.P., India, pp. 62-68.

Ong, C.K., 1984. The influence of temperature and water deficits on the partitioning of dry matter in groundnut (*Arachis hypogaea* L.). J. Exp. Bot., 35: 746-755.

Osiru, D.S.O. and Willey, R.W., 1972. Studies on mixtures of dwarf sorghum and beans (*Phaseolus vulgaris*) with particular reference to plant population. J. Agric. Sci., Camb., 79: 531-540.

Trenbath, B.R., 1976. Plant interactions in mixed crop communities. In: R.I. Papendick, P.A. Sanchez and G.B. Triplett (Editors), Multiple Cropping. Am. Soc. Agron. Spec. publ. no. 27, Madison Wis, pp. 129-169.

Willey, R.W., 1979. Intercropping - its importance and research needs. Part 1. Competition and yield advantages. Field Crop Abstracts, 32 (1): 1-10.
Willey, R.W. and Natarajan, M., 1980. Some aspects of resource use in sorghum/pigeonpea intercropping. Indian J. Genet., 40 (A): 16-26.